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Maternal Modulation of Natal Dispersal in a Passerine Bird: An Adaptive Strategy to Cope with Parasitism?

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ABSTRACT: The decision of how far to disperse from the natal territory has profound and long-lasting consequences for young animals, yet the optimal dispersal behavior often depends on environmental factors that are difficult or impossible to assess by inexperienced juveniles. Natural selection thus favors mechanisms that allow the adaptive and flexible adjustment of the offspring's dispersal behavior by their parents via either paternal or maternal effects. Here we show that different dispersal strategies maximize the reproductive success of young great tits (*Parus major*) originating from a parasite-infested or a parasite-free nest and demonstrate that differential transfer of maternal yolk androgens in response to parasitism can result in a modification of the offspring's dispersal behavior that appears adaptive. It demonstrates that prenatal maternal effects are an important yet so far neglected determinant of natal dispersal and highlights the potential importance of maternal effects in mediating coevolutionary processes in host-parasite systems.

Keywords: coevolution, host-parasite interactions, life history, maternal effects, maternal hormones, natal dispersal.

Natal dispersal is a key trait for many ecological and evolutionary processes influencing, for example, the genetic and social structuring within and gene flow between populations (Clobert et al. 2001). Although various environ-

mental and social factors have been associated with natal dispersal (reviewed in Clobert et al. 2001) and two recent studies reported evidence for a genetic basis of variation in individual dispersal behavior (Hansson et al. 2003; Pasinelli et al. 2004), the process of natal dispersal remains poorly understood (e.g., Massot and Clobert 2000).

The optimal dispersal strategy of young animals depends on the current or future environmental conditions, which require an individual to adaptively adjust its dispersal behavior in response to these factors (i.e., adaptive phenotypic plasticity). The optimal behavior may, however, depend on environmental cues that are difficult or impossible to assess by the individual itself, in particular, for inexperienced juveniles (De Witt et al. 1998), favoring mechanisms that allow the adaptive and flexible adjustment of the offspring's dispersal behavior by their parents (i.e., transgenerational phenotypic plasticity) via either maternal or paternal effects (e.g., Taborsky 2006).

Parental and, in particular, maternal effects have been shown to have a major impact on various offspring traits, including morphology, physiology, behavior, and reproductive success (reviewed in Mousseau and Fox 1998). Although they would provide an excellent means to adjust offspring dispersal according to environmental and social factors perceived by the mother, the role of maternal effects in shaping offspring dispersal is poorly understood (Massot and Clobert 2000; Dufty and Belthoff 2001; Ims and Hiermann 2001; but see Massot and Clobert 1995, 2000; De Fraipont et al. 2000; Meylan et al. 2002), and the demonstration of their adaptive value is lacking.

Although maternal effects can be mediated in many different ways—either before or after the young are born—in oviparous species, differential transfer of maternally derived androgens into the egg yolk is a particularly important mediator of the offspring's phenotype (reviewed in Groothuis et al. 2005). Maternal yolk androgens promote, for example, the offspring's embryonic development (Eising et al. 2001), postnatal growth (Schwabl 1996; Eising et al. 2001), and competitiveness in the nest (Schwabl 1996; Lipar and Ketterson 2000; Eising and Groothuis 2003). While so far most research has focused on the short-term effects of maternal

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yolk hormones on embryonic and nestling development, recent research also addressed the long-term consequences. These studies found surprisingly strong effects of exposure to different levels of yolk hormones on the birds' performance postfledging, influencing, for example, their social status (Schwabl 1993), their aggressive behavior almost 1 year after hatching (Strasser and Schwabl 2004; Eising et al. 2006), and potentially also their explorative behavior and dispersal (Dingemanse et al. 2003).

In host-parasite systems, the relative dispersal distance of hosts and their parasites can shape coevolutionary processes, including adaptation to the local parasite community (Gandon et al. 1996; Gandon 2002) and the evolution of parasite virulence (Boots and Sasaki 1999). Depending on the specific host-parasite system and environmental, spatial, and temporal variation in the risk of parasitism (Boulinier et al. 2001), different optimal dispersal strategies are thus expected to maximize fitness for parasite-infested and parasite-free hosts (Boulinier et al. 2001). From an evolutionary perspective, a parental modulation of offspring dispersal behavior might thus be of particular importance in such systems. A recent study by Van de Castele (2002) indeed documented evidence for transgenerational plasticity in dispersal behavior in response to parasitism: the natal dispersal distance of young great tits (*Parus major*) was influenced by the tick infestation status of their parents. The proximate mechanisms and the fitness consequences of this parental modification, however, remained unknown.

We have previously shown in another great tit population that female birds deposited lower concentrations of yolk androgens into their eggs when their nest was infested with ectoparasitic hen fleas (*Ceratophyllus gallinae*) before egg laying, compared with females that laid their eggs in a parasite-free nest (Tschirren et al. 2004). As yet, the adaptive significance of this behavior is unknown (Tschirren et al. 2005).

Here we investigate whether differential maternal transfer of yolk androgens in relation to parasitism (Tschirren et al. 2004) might result in differential dispersal patterns in offspring and could act as an adaptation to parasitism (Gandon et al. 1996; Boulinier et al. 2001; Gandon 2002). Thereto, we first describe optimal dispersal strategies of great tits in relation to parasitism, subsequently test for the role of maternal yolk androgens in shaping offspring natal dispersal, and, finally, discuss the potential adaptive significance of this transgenerational phenotypic plasticity.

Material and Methods

Study Place and Species

The study was performed in a great tit population breeding in nest boxes in the "Forst," a forest consisting mainly of

beech (*Fagus sylvatica*) and spruce (*Picea abies*), near Bern, Switzerland (46°54'N, 7°17'E/46°57'N, 7°21'E). The great tit is a small hole-nesting passerine (16–20 g) and one of the main hosts of the ectoparasitic hen flea *Ceratophyllus gallinae* (Tripet and Richner 1997). Hen fleas live in the nest material and suck blood from nestlings and adults. They hibernate in old nests and can already be present in large numbers at the start of the host's egg laying period (Tripet and Richner 1999). Hen fleas impair host fitness by affecting growth, survival, and future reproduction (Richner et al. 1993; Fitze et al. 2004a, 2004b).

Early Parasite Exposure, Natal Dispersal, and Reproductive Success

In a 4-year experimental study (1997–2000), we investigated different optimal dispersal strategies of young great tits in relation to parasitism, that is, the interaction effect between parasite exposure during the nestling period and the natal dispersal distance on the reproductive success of locally recruited birds. Twelve experimental plots consisting of 32 nest boxes each were established, and each plot was split in two patches consisting of 16 boxes. Patches within plots were randomly assigned to be infested with ectoparasitic hen fleas or were kept free of parasites during the four experimental years (Fitze et al. 2004b). An additional 88 boxes were established in the forest surrounding the plots. These boxes were randomly assigned to be parasite infested or parasite free in each year of the experiment to control for potential nonrandom phenotype distribution in the patch design (Fitze et al. 2004a). We determined clutch size and the number of fledglings produced in each brood during this 4-year period. Nestlings were individually ringed with aluminium rings, and breeding adults were captured while feeding 13-day-old nestlings in their nest box for identification, allowing for the assessment of local recruitment, reproductive success, and natal dispersal distance, that is, the distance the recruited birds moved between their birthplace and the site of their first reproduction (Greenwood 1980; Fitze et al. 2004b). Since breeding dispersal is insignificant in our study population (B. Tschirren and P. S. Fitze, personal observation; see also, e.g., Greenwood and Harvey 1982), the natal dispersal distance is a good description of an individual's dispersal behavior.

Yolk Testosterone and Parasite Manipulation

Since we have shown in an earlier study that great tit females differentially transfer yolk hormones into the eggs in response to parasites (Tschirren et al. 2004), we directly manipulated yolk testosterone concentrations in the eggs of the same population in 2002 to test whether differential

hormone deposition by the mother can adaptively shape the dispersal behavior of the offspring in relation to parasitism. After clutch completion (i.e., 1 day after the last egg was laid), we manipulated the yolk testosterone concentration as described by Tschirren et al. (2005). We injected all eggs of a clutch with either 30 ng of testosterone (17 β -hydroxy-4-androsten-3-one; Fluka, Switzerland) dissolved in 5 μ L of sesame oil or 5 μ L of sesame oil as a control. The dose of injected testosterone was similar to the highest concentrations of yolk testosterone found in previously analyzed great tit eggs from the same population (Tschirren et al. 2004). We injected a total number of 623 eggs from which 500 nestlings hatched. The overall hatching success was 80.3%, and it was not significantly different between testosterone-injected (81.4% hatched) and control eggs (79.2% hatched; $\chi^2 = 0.473$, $P = .492$, $N = 623$; Tschirren et al. 2004).

One day after hatching, nestlings from a control and a testosterone-injected clutch with the same hatching date and a similar brood size were partially exchanged. Nestlings were ranked in their original nest according to body mass and then alternately assigned to stay in their nest or to be transferred to the partner nest. For identification, we individually marked nestlings by clipping down feathers. After the cross-fostering, all nests contained nestlings of both treatment groups (originating from testosterone-injected and control eggs). This design thus ensured that both treatment groups had the same potential for dispersal within the study population and the same potential of being recorded as a local recruit the following year (Van Noordwijk 1984).

Before placing the nestlings back in the nest box, we heat-treated the nest material of all nests in a microwave oven (Richner et al. 1993) to kill all naturally present parasites. One randomly chosen nest of each cross-foster pair was then experimentally reinfested with 40 female and 20 male hen fleas while the other nest remained free of parasites (Richner et al. 1993). The hen fleas used for the infestation were extracted from old nests collected within the study area at the start of the breeding season. Eight days posthatching, nestlings were ringed with aluminium rings, and 15 days posthatching, we measured their body mass. Mortality during the nestling period was not significantly different between treatment groups ($\chi^2 = 2.828$, $P = .093$, $N = 500$), and at the end of the nestling period, a total of 240 nestlings originating from testosterone-manipulated and 248 nestlings originating from control eggs fledged.

Natal Dispersal

In the year after the experimental manipulation of yolk testosterone in the eggs, we captured all breeding birds in

the study area within their nest box while feeding 13-day-old nestlings. We measured body mass and metatarsus length of adult birds (Svensson 1992) and determined their natal dispersal distance.

Statistical Analyses

Early Parasite Exposure, Natal Dispersal, and Reproductive Success. For the analysis of the interaction effect between parasite exposure during the nestling period and the recruits' natal dispersal distance on their reproductive success, that is, the number of eggs laid and the number of fledglings produced, we used a general linear model (GLM) containing the parasite treatment of the rearing nest, the recruit's sex, the recruits' natal dispersal distance, and the interaction between parasite treatment and natal dispersal distance (for details, see Fitze et al. 2004b).

Because the experiment was performed over a 4-year period, birds born in the first year of the study had the chance to produce more offspring during the study period than birds born at the end of the study. This was accounted for by including the number of possible breeding events and the number of clutches produced as covariates into the model. During the study period, parasite manipulations were performed within the study population for another project. Since earlier studies have shown that parasites reduce the reproductive success of adult great tits (e.g., Richner et al. 1993; Fitze et al. 2004a, 2004b), we included the number of broods produced in a parasite-infested nest as a covariate in the final model to control for potentially confounding effects (for details, see Fitze et al. 2004b).

Yolk Testosterone Manipulation and Natal Dispersal. The effect of the yolk testosterone manipulation on the recruits' natal dispersal distance was analyzed with a GLM including hormone treatment, parasite treatment, and sex of the recruited birds as fixed effects. The recruitment rate of fledged birds in relation to the hormone manipulation, the parasite treatment, and the interaction between hormone manipulation and parasite treatment was analyzed by logistic regression.

Mean values of recruits originating from the same nest and the same treatment group were used in all analyses to control for nonindependence of these data. All possible interactions were included in the analyses and were backward eliminated from the final models if nonsignificant. All tests were two tailed, with a significance level set at $P \leq .05$. Residuals of the models were normally distributed and homoscedastic. Means \pm 1 SE are presented. Statistical analyses were performed using JMP IN 4.0 (Sall and Lehmann 1996).

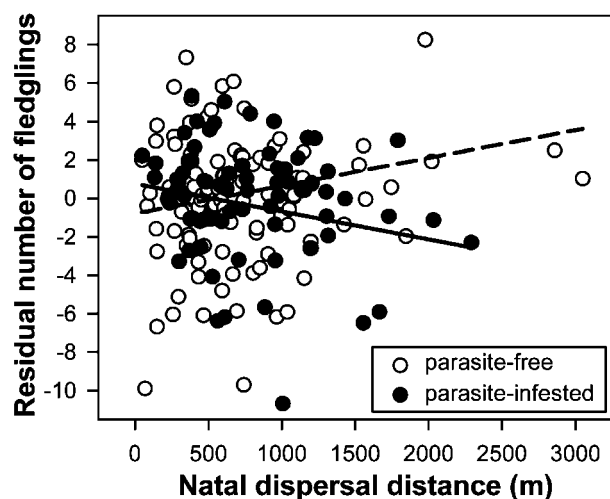


Figure 1: Number of fledglings produced by birds that grew up in a parasite-free nest (open circles and dashed line) or a nest infested with ectoparasitic hen fleas (solid circles and solid line) in relation to their natal dispersal distance. Residuals of the model without the interaction between parasite treatment and natal dispersal distance are shown.

Results

Natal Dispersal Distance and Reproductive Success

We found a statistically significant interaction effect of the parasite treatment of the rearing nest and the natal dispersal distance on the recruits' reproductive success (number of eggs produced: $F = 7.126$, $df = 1, 172$, $P = .008$; number of fledglings produced: $F = 5.534$, $df = 1, 177$, $P = .020$). In birds that grew up in a parasite-infested nest, the number of eggs laid and the number of fledglings produced decreased with increasing natal dispersal distance (eggs: $b = -0.0008$; fledglings: $b = -0.0012$), while in recruits originating from a parasite-free nest, the relationship between natal dispersal distance and reproductive success was positive (eggs: $b = 0.0004$; fledglings: $b = 0.0006$; fig. 1).

Yolk Testosterone and Natal Dispersal Distance

In a second step, we analyzed the role of maternal yolk androgens in shaping the offspring's dispersal behavior. We found that recruits originating from eggs with experimentally elevated yolk testosterone concentrations dispersed significantly longer distances (+44%) compared with control-injected birds (hormone manipulated birds: $1,070.5 \pm 132.4$ m [$N = 26$]; controls: 744.1 ± 89.1 m [$N = 19$]; $F = 4.093$, $df = 1, 42$, $P = .0495$; fig. 2).

We further found a tendency for birds reared in a flea-infested nest to disperse shorter distances than recruits

originating from a parasite-free nest (flea infested: 708.5 ± 115.1 m [$N = 13$]; parasite free: $1,023.8 \pm 111.3$ m [$N = 32$]; $F = 3.287$, $df = 1, 42$, $P = .0770$). Natal dispersal distance was not significantly different between male and female recruits in this study (females: 889.1 ± 117.9 m [$N = 21$]; males: 970.9 ± 130.3 m [$N = 24$]; $F = 0.224$, $df = 1, 41$, $P = .638$), and none of the interactions between hormone treatment, parasite treatment, and sex explained a significant amount of variation in dispersal distance (all $P > .250$). Natal dispersal distance was not significantly influenced by the recruit's body mass as a nestling ($F = 1.249$, $df = 1, 42$, $P = .270$), its body mass as an adult ($F = 0.088$, $df = 1, 42$, $P = .769$), or its body size (metatarsus length; $F = 0.192$, $df = 1, 42$, $P = .663$). The overall local recruitment rate was 9.2%. It was not significantly influenced by the hormone treatment ($\chi^2 = 1.38$, $P = .240$, $N = 488$), the parasite treatment ($\chi^2 = 0.60$, $P = .438$, $N = 488$), or the interaction between parasite and hormone treatment ($\chi^2 = 0.03$, $P = .869$, $N = 488$).

Discussion

The relative dispersal distance of hosts and their parasites can have profound consequences for coevolutionary processes in host-parasite systems (Gandon et al. 1996; Boulinier et al. 2001; Gandon 2002). The optimal dispersal behavior of an individual thus often depends on parasite

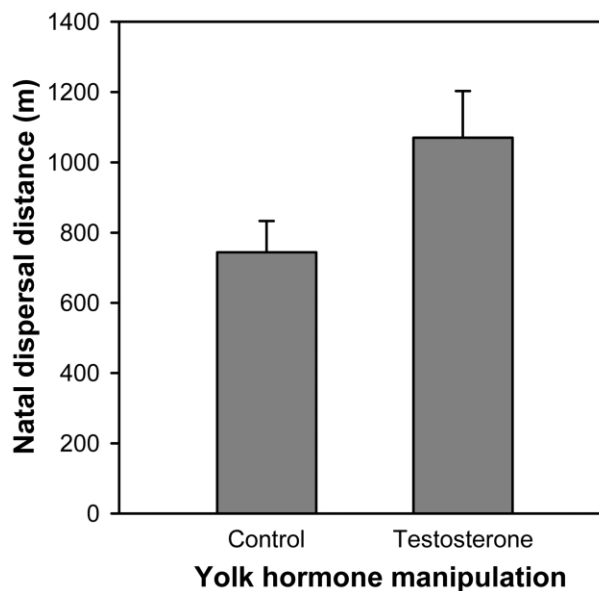


Figure 2: Natal dispersal distance of recruits originating from testosterone-injected ($N = 26$) and control-injected ($N = 19$) eggs. Means + 1 SE are shown.

abundance. In cliff swallows (*Petrochelidon pyrrhonota*), for example, longer dispersal distances were observed when the parasite load was high in the natal territory. This parasite-dependent dispersal pattern might reflect an adaptive host strategy, since by abandoning a heavily infested nest site, cliff swallows may reduce the negative parasite impact on both themselves and their offspring (Brown and Brown 1992). Alternatively, however, it might reflect a host manipulation by the parasite (Lion et al. 2006).

In great tits, the opposite pattern was observed, and birds that were exposed to parasites—in this case, ectoparasitic hen fleas—during the nestling stage dispersed shorter distances compared with parasite-free birds (Heeb et al. 1999; but see Fitze et al. 2004b), a trend that was also observed in this study. Here we show that relatively short dispersal distances in the presence of hen fleas are adaptive: the reproductive success of birds originating from parasite-infested nests decreased with increasing natal dispersal distance, while the opposite pattern was observed for local recruits originating from parasite-free nests. Beneficial effects of short dispersal distances in the presence of parasites, as demonstrated here, might reflect a strategy that favors adaptive host responses to the local parasite community (Heeb et al. 1998; Boulinier et al. 2001; Gasparini et al. 2001; Buechler et al. 2002) or a lower ability of parasite-infested birds to cope with a new environment (e.g., Pärt 1994). However, irrespective of the proximate mechanism underlying the negative relationship between dispersal distance and reproductive success in parasite-infested birds, parents rearing an infested brood gain higher fitness by promoting their offspring's philopatry.

Parents could promote offspring philopatry via parental behavior after fledging (e.g., by reduced aggression directed toward offspring after independence); however, prenatal maternal effects also are good candidates for the modification of the young's dispersal behavior in response to parasites (e.g., Massot and Clobert 1995, 2000; De Fraipont et al. 2000; Meylan et al. 2002; Van de Castele 2002). Tschirren et al. (2004) showed that female great tits transferred lower concentrations of yolk androgens into the eggs when their nest was infested with ectoparasitic hen fleas compared with unexposed control females. This differential deposition of yolk androgens might directly shape the offspring's resistance to parasites because of potential immunosuppressive effects of exposure to high concentrations of yolk androgens during embryonic development (Grossman 1985; Groothuis et al. 2005; Müller et al. 2005; Tschirren and Richner 2006). However, an experimental manipulation of yolk testosterone and subsequent measure of both the cell-mediated immune response and the susceptibility to hen fleas revealed no such direct effect in this system (Tschirren et al. 2005). This study, however,

suggests that the transfer of low concentrations of yolk androgens into the eggs in the presence of parasites might play an important role in modulating the offspring's dispersal behavior instead. Recruited birds originating from an egg with experimentally elevated yolk testosterone concentrations dispersed significantly longer distances (+44%) between their rearing place and the place of their first reproduction. The deposition of low concentrations of yolk androgens into the eggs in the presence of hen fleas (Tschirren et al. 2004) might thus be a female strategy to promote philopatry of parasitized offspring and thus to increase her offspring's and thereby her own fitness.

Prenatal exposure to androgens has previously been suggested to promote natal dispersal in mammals (Dufty and Belthoff 2001). In gray-sided voles, females from litters with a high proportion of males were more likely to disperse than females from other litters (Ims 1989, 1990), suggesting that prenatal exposure of females to their brothers' testosterone predisposed them to disperse. Our experimental study shows that the hormonal environment experienced during embryonic development can also regulate the level of natal dispersal in birds. It indicates that females of a wide range of taxa can modify the dispersal behavior of their offspring according to the environmental or social conditions experienced during reproduction by differential transfer of androgens into the eggs or altering the embryo's exposure to androgens in utero.

In conclusion, our study demonstrates that maternal effects are a potentially important determinant of natal dispersal, yet so far they have been largely neglected in natal dispersal research. Future studies should thus assess the generality and relative importance of this transgenerational effect on natal dispersal in other systems and estimate the selection acting on the plasticity of maternal resource allocation in response to environmental or social factors to evaluate its adaptive nature.

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